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CONTRIBUTIONS TO ENTOMOLOGY

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Research Article

Taxonomic position of the fossil ant genus *Stiphromyrmex* Wheeler (Hymenoptera: Formicidae), with the first description of its queen

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Abstract

The previously unknown queen of *Stiphromyrmex robustus* (Mayr, 1868) is described. The taxonomic position of the fossil genera *Stiphromyrmex* Wheeler, 1915, *Enneamerus* Mayr, 1868, and *Thanacomyrmex* Chény, Wang & Perrichot, 2019 is discussed, and their placement in the *Myrmecina* genus-group of the tribe Crematogastrini Forel, 1893 is confirmed. A key for the identification of fossil genera and species of this genus-group is provided.

Zusammenfassung

Die bisher unbekannte Königin von *Stiphromyrmex robustus* (Mayr, 1868) wird beschrieben. Die taxonomische Stellung der fossilen Gattungen *Stiphromyrmex* Wheeler, 1915, *Enneamerus* Mayr, 1868, und *Thanacomyrmex* Chény, Wang und Perrichot, 2019, wird diskutiert und ihre Zugehörigkeit zur Gattungsgruppe *Myrmecina* des Stammes Crematogastrini Forel, 1893, wird bestätigt. Ein Schlüssel zur Identifizierung der fossilen Gattungen und Arten dieser Gattungsgruppe wird erstellt.

Key Words

Amber, Europe, key, Late Eocene, *Myrmecina* genus-group, paleontology

Schlüsselwörte

Bernstein, Europa, *Myrmecina*-Gattungsgruppe, Paläontologie, Schlüssel, Spät-Eozän

Introduction

The ant fauna of Late Eocene (Priabonian age, 37.8–33.9 Ma) European ambers (i.e., Baltic, Bitterfeld, Danish, and Rovno) is the richest of any local fossil myrmecofauna in the world: 70 extinct and extant genera from 12 extant subfamilies and 204 extinct species have been recorded, and at least 20 new species and several genera are still awaiting a formal description (AntWeb 2025; unpublished personal data). Among these, the subfamily Myrmicinae, with 26 genera and 83 described species, is the most diverse (Dlussky and Rasnitsyn 2009; Barden 2017; Radchenko 2023, 2024; Radchenko et al. 2024, 2025; Boudinot et al. 2024; Radchenko and Khomych 2025).

Wheeler (1915) established the monotypic extinct myrmicine genus *Stiphromyrmex* with the type species

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Stigmomyrmex robustus (Mayr, 1868), described from Baltic amber. *Stiphromyrmex* is clearly distinguished from related genera found in the ambers mentioned by its 12-segmented antennae instead of the 9-segmented in *Enneamerus* Mayr, 1868, and the 11-segmented antennae in *Pristomyrmex* Mayr, 1866 and *Thanacomyrmex* Chény, Wang & Perrichot, 2019. This genus is otherwise quite peculiar, its main diagnostic features being: total length of 3.25–3.50 mm; head without antennal scrobes; eyes of moderate size, situated in front of the midlength of the sides of the head; frontal carinae absent; frontal lobes poorly developed, only partly covering the antennal sockets, and toruli not concealed by the frontal lobes; median part of clypeus flattened, delineated laterally by coarse longitudinal carinae, anterior clypeal margin with paired long setae, no medial seta present; antennae 12-segmented, scape short, far from reaching the occipital margin, funiculus with a well-developed three-segmented apical club; mandibles with distinct masticatory margin, armed with two larger apical teeth followed by two small denticles; palp formula 4, 3; mesosoma compact, short, and stout, promesonotum convex, promesonotal suture and metanotal groove absent; propodeum with massive curved spines directed upward and backward at an angle of ca. 55°; femora and tibiae somewhat incrassated, meso- and metatibiae with a well-developed simple spur; head and mesosoma with coarse foveolate sculpture (Fig. 3).

Recently, one of the co-authors (HWR) discovered a queen in a piece of Baltic amber that matches the main diagnostic features of workers of *Stiphromyrmex robustus*. Here, this queen morphotype is described for the first time. We also discuss the taxonomic position of the genus *Stiphromyrmex*, and we compile a key to the identification of amber genera and species from the *Myrmecina* genus-group, to which *Stiphromyrmex* belongs.

Material and methods

We investigated the queen of *Stiphromyrmex robustus*, fossilized in a piece of Baltic amber, as well as the neotype worker of this species that was designated recently by Radchenko and Dlussky (2017b).

The original photographs were taken with a Leica Z16 APO microscope equipped with a Canon EOS 70D camera and processed by LAS Core software, and with flash lighting and a P-51 Camlift Driver ver. 2.6.1 controlling a Canon EOS K2-SC camera.

The specimens were measured using a Leica MZ6 stereomicroscope with an ocular micrometer at a maximum magnification of ×100. Not all features of the specimen examined were properly measurable, so we measured only well-visible details (calculated to an accuracy of 0.01 mm), particularly:

HL maximum length of the head in dorsal view, measured in a straight line from the anteriormost point of the clypeus to the midpoint of the occipital margin;

SL maximum length of the scape, measured in a straight line from its apex to the articulation with the condylar bulb;

OL maximum diameter (length) of the eye;

OW minimum diameter (width) of the eye;

GL length of the genae, measured from the anterior margin of the eyes to the articulation with the mandible;

MdL length of the mandible, measured from its tip to articulation with the head;

ML diagonal length of the mesosoma (seen in profile), measured from the anterior end of the neck shield to the posterior margin of the propodeal lobes;

MH height of the mesosoma, measured from the upper level of the scutum perpendicularly to the level of the lower margin of the mesopleuron;

PL maximum length of the petiole, measured from the posterodorsal margin of the petiole to the articulation with the propodeum;

PH maximum height of the petiole in profile, measured from the uppermost point of the petiolar node perpendicularly to the lowest point of the petiole;

PW maximum width of the petiole in dorsal view;

PPL maximum length of the postpetiole between its visible anterior and posterior margins;

PPH maximum height of the postpetiole in profile from the uppermost to the lowermost points, measured perpendicularly to the tergosternal suture;

PPW maximum width of the postpetiole in dorsal view;

HTL maximum length of the metatibia;

HFL maximum length of the metafemur;

ESL maximum length of the propodeal spine in profile, measured along the spine from its tip to the deepest point of the propodeal constriction at the base of the spine;

ESD distance between the tips of the propodeal spine in dorsal view.

The approximate total length is calculated as the sum of HL + ML + PL + PPL + length of the gaster.

For simplicity, we give ratios of various measurements (e.g., HL/HW) rather than naming and abbreviating various indices (e.g., CI – cephalic index).

Results

Class Insecta Linnaeus, 1758
Order Hymenoptera Linnaeus, 1758
Family Formicidae Latreille, 1802
Subfamily Myrmicinae Lepeletier de Saint-Fargeau, 1835
Genus *Stiphromyrmex* Wheeler, 1915

***Stiphromyrmex robustus* (Mayr, 1868)**

Material examined. Queen, complete specimen, Poland, Gulf of Gdansk, Baltic amber, collection number

BS 056/065; currently, until the end of Russia's war against Ukraine, it is stored in the private collection of H.-W. Ribbecke, Germany, and after that it will be transferred to the I.I. Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine, Kiev; worker, neotype, Poland, Gulf of Gdansk, Baltic amber, No. 8483, deposited in the Muzeum Ziemi of the Polish Academy of Sciences, Warsaw.

First description of queen. Figs 1A, B, 2A, B. Body length 5.5 mm. Head width not properly measurable in specimen, but head appears slightly elongated, with almost straight and subparallel sides, narrowly rounded occipital corners and straight occipital margin. Eyes of moderate size, elongate-oval, situated in front of midlength of sides of head. Ocelli barely visible due to nature of sculpture (see below). Frontal carinae absent;

Figure 1. Queen of *Stiphromyrmex robustus*, specimen No. BS 056/065. **A.** Right dorso-lateral view; **B.** Left lateral view.

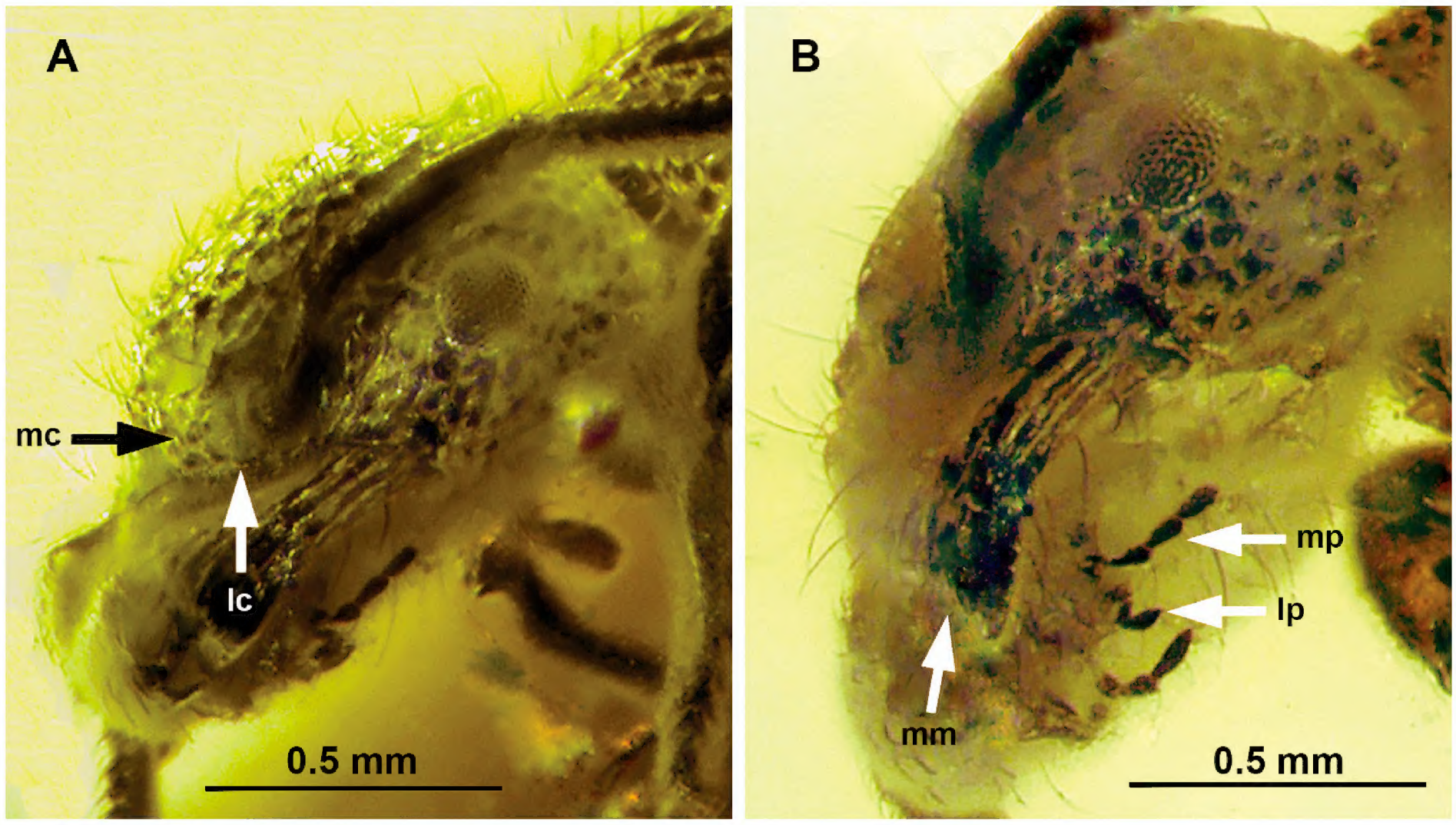

Figure 2. Queen of *Stiphromyrmex robustus*, specimen No. BS 056/065. **A.** Head, lateral view; **B.** Head, ventro-lateral view; lc – lateral part of clypeus; lp – labial palp; mc – median part of clypeus; mm – masticatory margin of mandible; mp – maxillary palp.

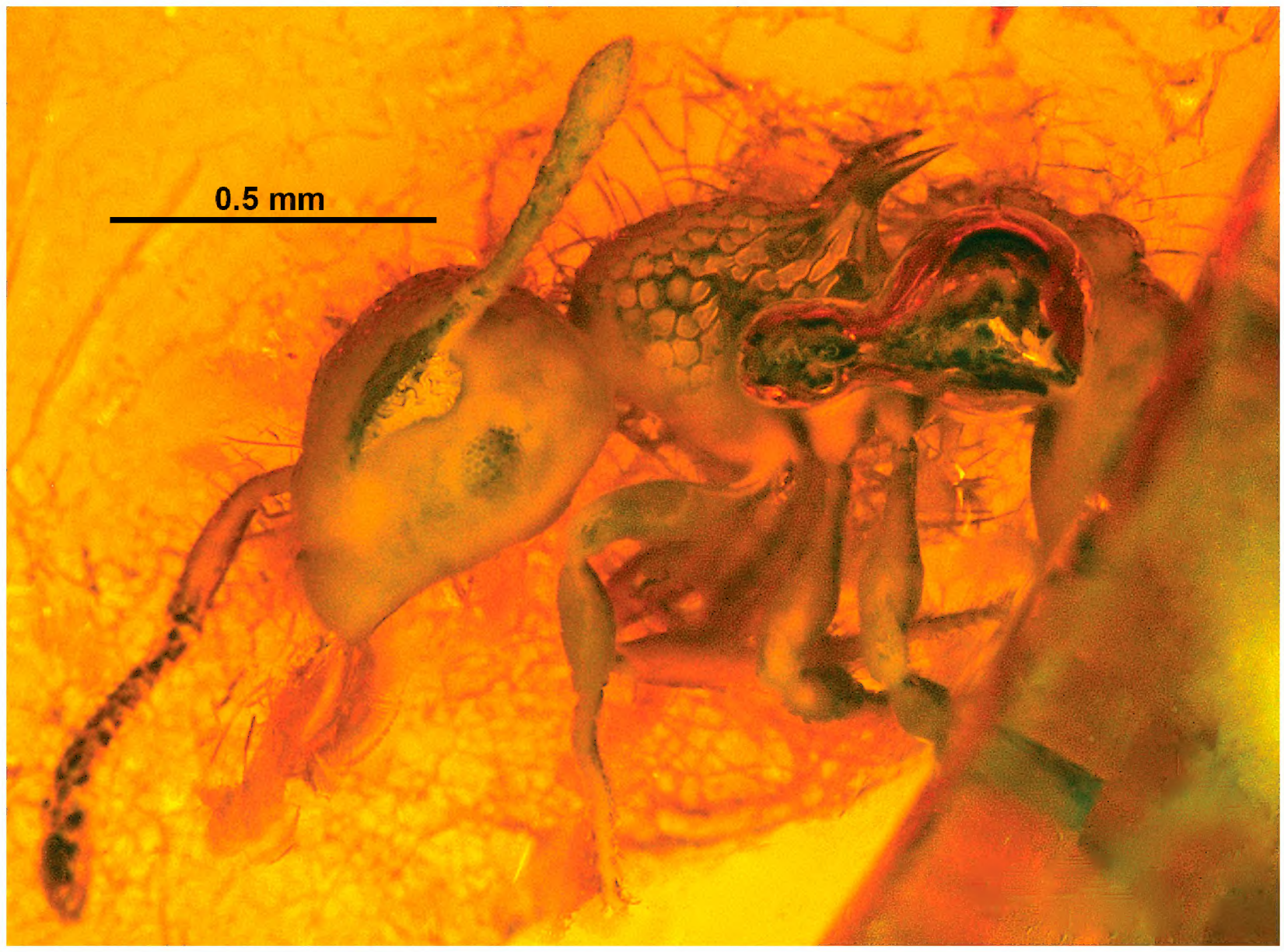

Figure 3. Neotype worker of *Stiphromyrmex robustus*, specimen No. 8483.

frontal lobes weakly developed, horizontal, antennal sockets mostly exposed and toruli not concealed by frontal lobes; antennal scrobes absent. Clypeus posteriorly rather widely inserted between frontal lobes, its median part flattened, delineated laterally by coarse longitudinal carinae, with three longitudinal costae each, terminated at the apices with sharp teeth; lateral parts of clypeus raised into a ridge in front of toruli; anterior clypeal margin with paired long setae, without medial seta, its median part almost straight. Mandibles rather long, with

distinct masticatory margin, armed with two large sharp apical teeth followed by two blunt tuberculate denticles. Maxillary palps 4-segmented, labial palps 3-segmented. Antennae 12-segmented, with distinct 3-segmented club. Antennal scape gradually curved at base and with no trace of lobe or carina, relatively short, far not reaching occipital margin. First funicular segment ca. twice as long as wide, 2nd–8th segments transverse, total length of 9th–11th segments subequal to total length of preceding segments.

Mesosoma short, high, and robust. Pronotum well developed, scutum slightly convex, scutellum flattened. Propodeal dorsum feebly convex, somewhat shorter than posterior surface, propodeal lobes slightly angulated but not pointed. Propodeal spines widened at the base, very long, ca. half of head length, curved down along their length, sharply pointed at apices, and subparallel (as seen from above). Petiole of moderate length and quite low, PL/PH 1.74, PL/HL 0.45; length of anterior peduncle subequal to length of node; anterior surface of node concave, its dorsum rounded, posterior surface somewhat convex, gradually sloping backwards; petiole ventrally with longitudinal lamella. Postpetiole subglobular, 1.35 times as wide as petiole. Legs of moderate length (HTL/ML 0.51, HFL/ML 0.67), femora and tibiae somewhat incrassated, pretarsal claws simple, arolia well developed. Meso- and metatibiae with well-developed simple spur.

Body coarsely sculptured. Entire head (except for clypeus), pronotum, scutum, scutellum and propodeal dorsum with big and deep foveae, that touch each other; mesopleura and sides of propodeum with very coarse longitudinal costae; petiolar node and postpetiole with less coarse costulate sculpture; base of first gastral tergite near postpetiole with short longitudinal costulae; gastral tergites with scattered piligerous pits or small foveae. Mandibles with longitudinal rugae.

Head and mesosoma with sparse, long erect and short suberect setae; petiolar node dorsum with two suberect setae; shorter suberect setae are visible only on ventral surface of postpetiole. All gastral sternites with quite numerous and long subdecumbent to suberect setae; first gastral tergite appears bare, pilosity on remaining tergites are hidden by whitish coating. Antennae and legs with abundant short subdecumbent pilosity.

Measurements (in mm) and ratios: HL 1.14, SL 0.73, OL 0.22, OW 0.17, GL 0.16, MdL 0.60, ML 1.46, MH 0.94, PL 0.52, PH 0.30, PW 0.26, PPL 0.39, PPH 0.33, PPW 0.35, HTL 0.74, HFL 0.98, ESL 0.55, ESD 0.52; SL/HL 0.64, OL/HL 0.19, OL/OW 1.31, OL/GL 1.42, MdL/HL 0.52, PL/PH 1.74, PL/PW 2.00, PL/HL 0.45, PPL/PPH 1.20, PPW/PW 1.35, ESL/HL 0.48, ESD/ESL 0.95, ML/MH 1.56, HTL/ML 0.51, HFL/ML 0.67.

Males unknown.

The studied queen possesses all the diagnostic features of the *Stiphromyrmex robustus* workers, differing from them by the structure of the mesosoma and sculpture of the mesopleura and sides of the propodeum, which are longitudinally coarsely costulate (compare Fig. 1 and Fig. 3). It undoubtedly belongs to this genus and most likely to *S. robustus*. However, we do not exclude that it may belong to another, as yet undescribed species of this genus, but we have no arguments in favor of this assumption. Therefore, for now, we classify it as *Stiphromyrmex robustus*.

Discussion

The taxonomic position of *Stiphromyrmex* is not yet definitively resolved. Wheeler (1915) placed this genus in the tribe Myrmicini Lepeletier de Saint-Fargeau, 1835, and considered it to be related to the Paleotropical genus *Pristomyrmex*. It should be noted that Wheeler (loc. cit.) treated this tribe too broadly and included many unrelated genera in it. Later, Dlussky and Fedoseeva (1988) treated *Stiphromyrmex* as incertae sedis in Myrmicinae, and more recently Bolton (1994, 1995, 2003) considered it incertae sedis in the tribe "Myrmecinini" Ashmead, 1905, which was simply repeated by Radchenko and Dlussky (2017b). Then Ward et al. (2015) synonymized many tribal names, including "Myrmecinini," with Crematogastrini Forel, 1893, and assigned *Stiphromyrmex* to this tribe.

The generic composition of the tribe "Myrmecinini" has changed over time (e.g., see Ashmead 1905; Emery 1914; Forel 1917; Emery 1924; Chapman and Capco 1951; Dlussky and Fedoseeva 1988), and as a result Bolton (2003) attributed four extant (*Acanthomyrmex* Emery, 1893; *Myrmecina* Curtis, 1829; *Perissomyrmex* M. Smith, 1949; and *Pristomyrmex*) and two extinct genera (*Enneamerus* and *Stiphromyrmex*) to this tribe. Finally, based on molecular phylogenetic analysis, Blaimer et al. (2018) established an informal *Myrmecina* genus-group within Crematogastrini, including all extant genera of the tribe "Myrmecinini" sensu Bolton (2003) with the addition of the genus *Dilobocondyla* Santschi, 1910, and supported the monophyly of this genus-group, with *Dilobocondyla* as sister to the other four genera.

However, morphologically the former tribe "Myrmecinini" (even without *Dilobocondyla*) is not so strictly defined, and its taxonomic position within the subfamily Myrmicinae remains somewhat uncertain (Bolton 2003). For example, Emery (1914, p. 37) noted about "Myrmecinini": *"Caratteri negativi; generi non rientranti in nessuna delle tribu seguenti"* [Negative characteristics; genera not belonging to any of the following tribes], and Bolton (2003) hesitated to assign "Myrmecinini" to any of the tribal groups he proposed.

Nevertheless, Bolton (loc. cit.) emphasized several specific features of the labrum as apomorphies of this tribe, but these features are practically invisible in most fossil specimens. At the same time, Emery (1924: 230) noted that *"Les parties latérales de l'épistome sont étroites et forment á leur bord postérieur une arête*

transversale, limitant, comme chez les Tetramoriini, la fosse antennaire" [The lateral parts of the clypeus are narrow and form a transverse ridge at their posterior edge, bordering, as in Tetramoriini, the antennal sockets]. Bolton (2003) confirmed this character and added several more.

As a result, the *Myrmecina* genus-group can be, at least tentatively, defined by the following characters: a) the lateral parts of the clypeus are raised into a ridge in front of the antennal insertions (similar to *Tetramorium* Mayr, 1855); b) the median part of the clypeus is broadly inserted between the antennal sockets; c) the frontal lobes are strongly reduced, so that the antennal sockets and toruli are largely or entirely exposed (except for *Myrmecina* and *Dilobocondyla*); d) the antennae have 9, 11, or 12 segments and a 3-segmented apical club.

Twenty-six Myrmicinae genera, both extant and extinct, are currently recorded from the Late Eocene European ambers, and workers and/or gynes are known for 21 of them (Wheeler 1915; Dlussky and Perkovsky 2002; Dlussky and Radchenko 2006a, b, 2011; Radchenko et al. 2007; Radchenko and Dlussky 2011, 2012, 2015; Chény et al. 2019; Radchenko 2023, 2024; Radchenko and Khomych 2025).

Among these, only four genera correspond to the proposed characteristics of the *Myrmecina* genus-group: the extinct *Enneamerus*, *Stiphromyrmex*, and *Thanacomyrmex*, and the extant *Pristomyrmex*. In particular, their frontal lobes are strongly reduced, and the antennal sockets are completely or almost completely exposed; at least the toruli are not concealed by the frontal lobes. The median portion of the clypeus is broadly inserted between the antennal sockets, and the lateral parts of the clypeus are raised into a ridge in front of the antennal sockets. They have already been assigned, at least tentatively, to the tribe "Myrmecinini" or, formally, to the *Myrmecina* genus-group of the tribe Crematogastrini (Bolton 2003; Blaimer et al. 2018; Chény et al. 2019), and we agree with this opinion.

In any case, the three fossil genera mentioned above already displayed some derived characters and cannot be considered the putative ancestors of any genera of the *Myrmecina* genus-group or even the stem of this group.

Below we compile a key to the identification of the genera and species attributed to the *Myrmecina* genus-group. Two species from Baltic amber are known in *Enneamerus* Mayr, 1868 (Radchenko and Dlussky 2017a); one species each from the same amber is known in *Stiphromyrmex* and *Thanacomyrmex*, and three species of *Pristomyrmex* Mayr, 1866 were found in Danish, Bitterfeld, and Rovno ambers (one species based on the male only) (Dlussky and Radchenko 2011; Radchenko and Dlussky 2018).

Key to identification of the amber genera and species from *Myrmecina* genus group

(workers)

1 Antennae 9-segmented; head dorsum with well-developed antennal scrobes (Fig. 4A, B) ***Enneamerus* Mayr, 1868**

– a) frons with 4–5 fine longitudinal rugae between frontal carinae level with the eyes, and with reticulation; antennal scape with long, abundant erect to suberect setae, which are distinctly longer than maximum width of scape (Fig. 4A) ***E. reticulatus* Mayr, 1868**

– b) frons with six coarse longitudinal costae between frontal carinae level with the eyes and with reticulation; antennal scape with shorter and less abundant suberect setae, which are not longer than maximum width of scape (Fig. 4B) ***E. costatus* Radchenko & Dlussky, 2017**

– Antennae 11- or 12-segmented; head dorsum without antennal scrobes (Figs 3, 5–7) **2**

2(1) Antennae 12-segmented (Figs 1A, B, 3) [One species is known: *S. robustus* (Mayr, 1868)] ***Stiphromyrmex* Wheeler, 1915**

– Antennae 11-segmented (Figs 5A, B, 6, 7) **3**

3(2) Central part of clypeus delineated by two longitudinal carinae, its anterior margin simple (Fig. 5B). Pronotum and petiole with spines, petiole subsessile (Fig. 5C) [One species is known: *T. hoffeinsorum* Chény et al., 2019] ***Thanacomyrmex* Chény et al., 2019**

– Central part of clypeus not delineated by longitudinal carinae, its anterior margin with two or three blunt teeth (Figs 6A, B, 7A). Pronotum and petiole unarmed, petiole distinctly pedunculate (Figs 6A, B, 7B) ***Pristomyrmex* Mayr, 1866**

– a) anterior clypeal margin medially with three teeth; propodeum with relatively long spines (Fig. 6A, B) ***P. rasnitsyni* Dlussky & Radchenko, 2011**

– b) anterior clypeal margin medially with two teeth (Fig. 7A); propodeum with short pointed teeth (Fig. 7B) ***P. elmesi* Radchenko & Dlussky, 2018**

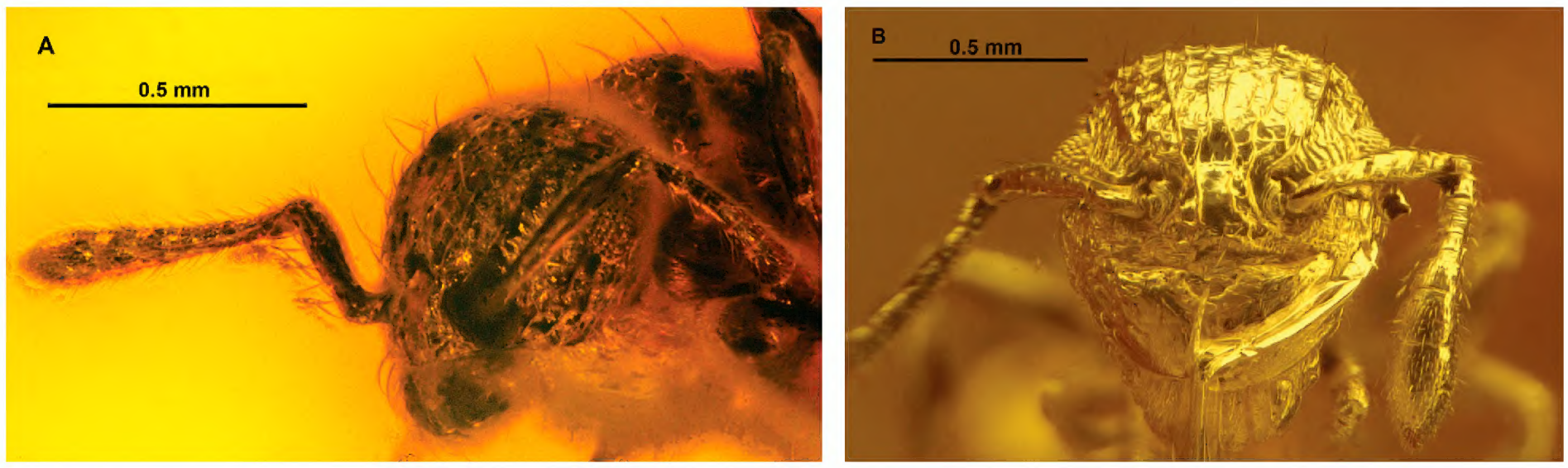

Figure 4. Workers of *Enneamerus*. **A.** *E. reticulatus*, head, specimen No. 15434; **B.** *E. costatus*, head, holotype worker, No. F-6763.

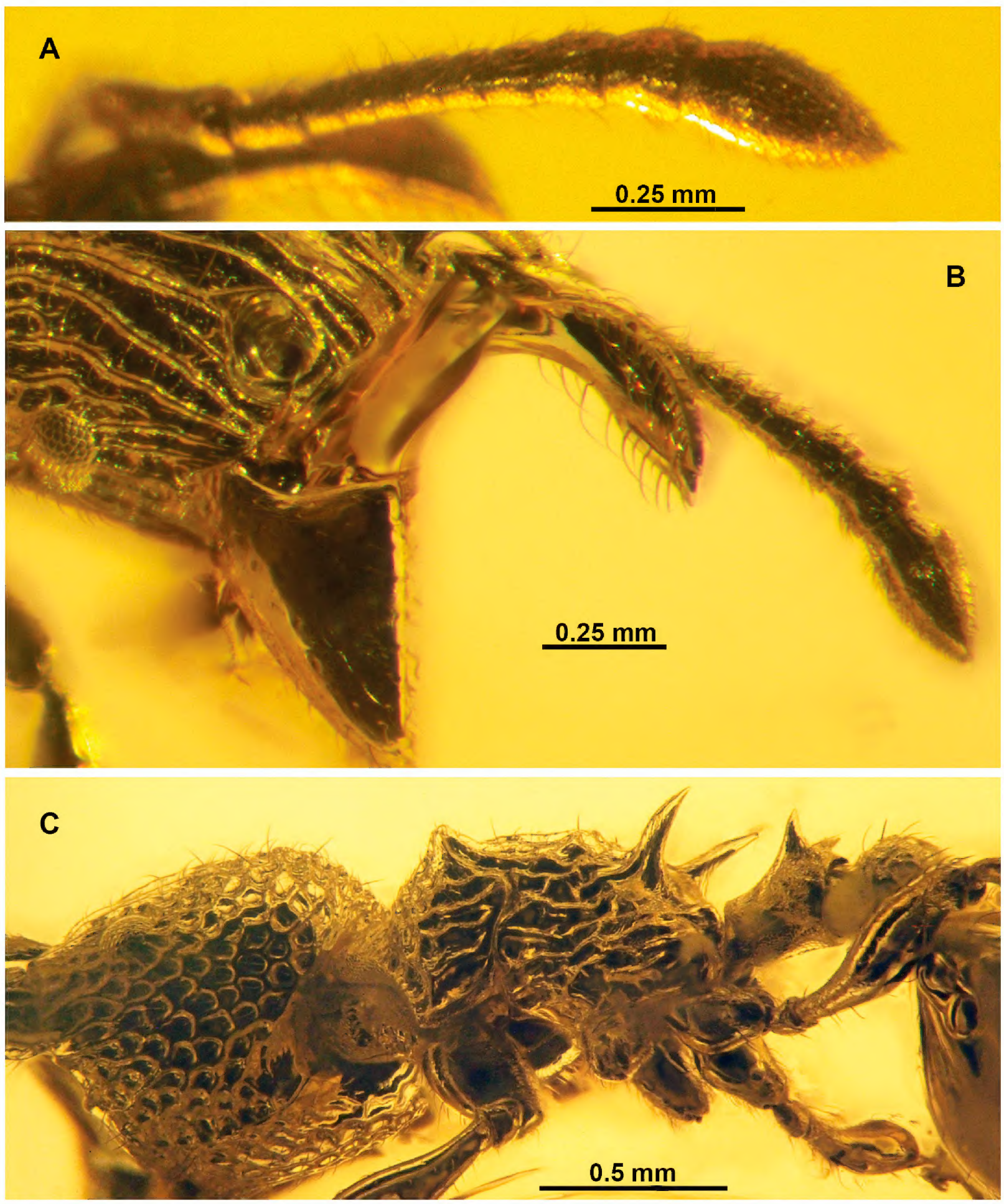

Figure 5. Holotype worker of *Thanacomyrmex hoffeinsorum*, No. 1628-6. **A.** Antenna; **B.** Anterior part of head; **C.** Head, mesosoma, and waist (photos by Vincent Perrichot).

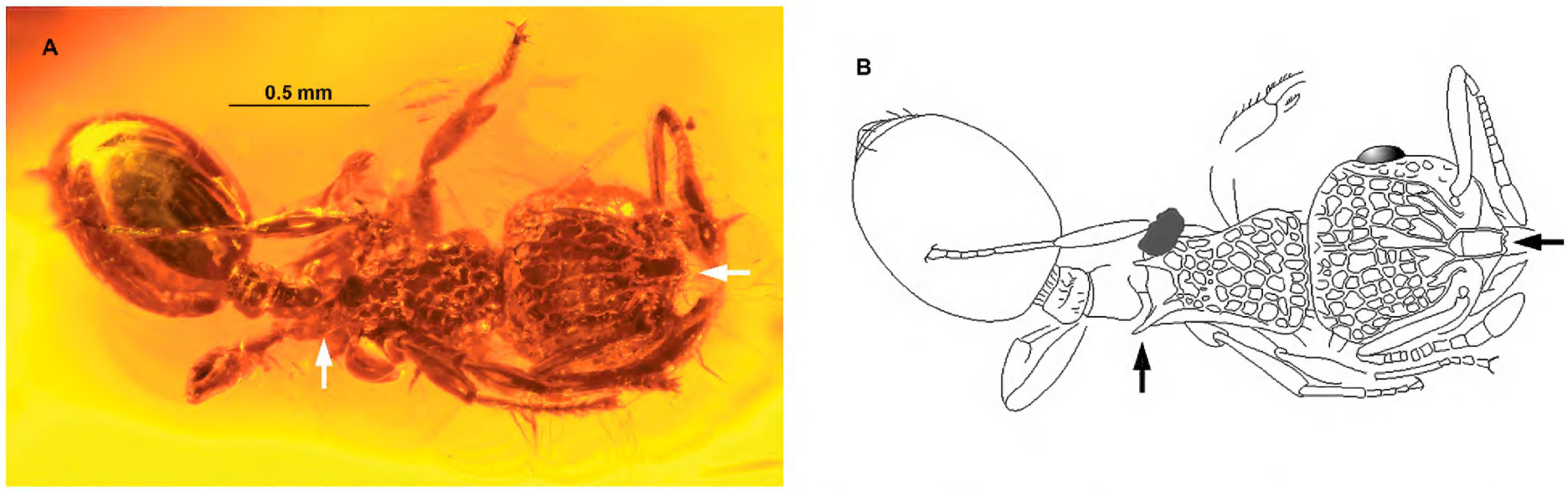

Figure 6. Holotype worker of *Pristomyrmex rasnitsyni*, No. 328. **A.** Photo of the holotype (photo by Alisa Perkovsky); **B.** Line drawing made based on photo (original); arrows indicate clypeal teeth and propodeal spine.

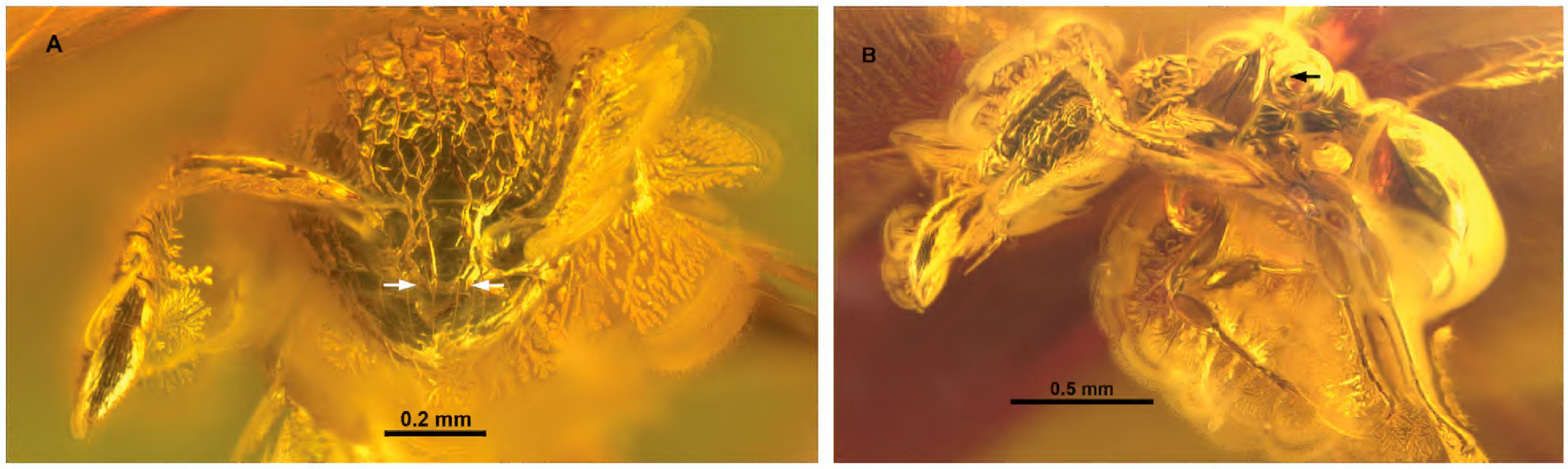

Figure 7. Holotype worker of *Pristomyrmex elmesi*, K-7248. **A.** Head, arrows indicate clypeal teeth; **B.** Body, arrow indicates propodeal tooth.

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References

André E (1895) Notice sur les fourmis fossiles de l'ambre de la Baltique et description de deux espèces nouvelles. Bulletin de la Société Zoologique de France 20: 80–84. https://antwiki.org/w/images/2/28/Andre_1895b.pdf

AntWeb (2025) Version 8.114. California Academy of Science. [online at] https://www.antweb.org [Accessed 18-11-2025]

Ashmead WH (1905) A skeleton of a new arrangement of the families, subfamilies, tribes and genera of the ants, or the superfamily Formicoidea. The Canadian Entomologist 37: 381–384. https://doi.org/10.4039/Ent37381-11

Barden P (2017) Fossil ants (Hymenoptera: Formicidae): ancient diversity and the rise of modern lineages. Myrmecological News 24: 1–30.

Blaimer BB, Ward PS, Schultz TR, Fisher BL, Brady SG (2018) Paleotropical diversification dominates the evolution of the hyperdiverse ant tribe Crematogastrini (Hymenoptera: Formicidae). Insect Systematics and Diversity 2: 1–14. https://doi.org/10.3161/00034541ANZ2024.74.4.015

Bolton B (1994) Identification guide to the ant genera in the World. Harvard University Press, Cambridge, Mass., 222 pp.

Bolton B (1995) A new general catalogue of the ants of the World. Harvard University Press, Cambridge-London, 504 pp.

Bolton B (2003) Synopsis and classification of Formicidae. Memoirs of the American entomological Institute 71: 1–370.

Boudinot BE, Bock BL, Weingardt M, Tröger D, Batelka J, Li D, Richter A, Poh H, Moosdorf OTD, Jandausch K, Hammel JU, Beutel RG (2024) Et latet et lucet: Discoveries from the Phyletisches Museum amber and copal collection in Jena, Germany. Deutsche Entomologische Zeitschrift 71: 111–176. https://doi.org/10.3897/dez.71.112433

Burnham L (1979) Survey of social insects in the fossil record. Psyche 85(1978): 85–134. https://doi.org/10.1155/1978/80816

Chapman JW, Capco SR (1951) Check list of the ants of Asia. Monographs of the Institute of Science and Technology, Manila, 1, 327 pp.

Chény C, Wang B, Perrichot V (2019) A new genus of myrmicine ant from Eocene Baltic amber. Comptes Rendus Palevol 18: 589–597. https://doi.org/10.1016/j.crpv.2019.05.005

Dalla Torre CG (1893) Catalogus Hymenopterorum, hucusque descriptorum systematicus et synonymicus 7. Lipsiae, 289 pp. https://doi.org/10.5962/bhl.title.8794

Dlussky GM, Fedoseeva EB (1988) Origin and early stages of the ant evolution (Hymenoptera: Formicidae). In: Ponomarenko AG (Ed.) Melovoj biocenoticheskij krizis i evolucija nasekomych. Nauka, Moskva, 70–144. [In Russian]

Dlussky GM, Perkovsky EE (2002) Ants (Hymenoptera, Formicidae) from the Rovno amber. Vestnik Zoologi 36(5): 3–20. [In Russian]

Dlussky G, Radchenko A (2006a) *Fallomyrma* gen. nov., a new myrmicine ant genus (Hymenoptera: Formicidae) from the Late Eocene European amber. Annales Zoologici 56(1): 153–157.

Dlussky GM, Radchenko A (2006b) New ant genus from the late Eocene European amber. Acta Palaeontologica Polonica 51: 561–567.

Dlussky GM, Radchenko AG (2011) *Pristomyrmex rasnitsyni* sp. n. – the first known fossil species of the ant genus *Pristomyrmex* Mayr (Hymenoptera, Formicidae) from the Late Eocene Danish Amber. Russian Entomological Journal 20: 251–254. https://doi.org/10.15298/rusentj.20.3.05

Dlussky GM, Rasnitsyn AP (2009) Ants (Insecta: Vespida: Formicidae) in the Upper Eocene amber of Central and Eastern Europe. Paleontological Journal 43: 1024–1042. https://doi.org/10.1134/S0031030109090056

Emery C (1914) Intorno alla classificazione dei Myrmicinae. Rendiconto delle Sessioni della R. Accademia delle Scienze dell'Istituto di Bologna (N.S.) 18: 29–42.

Emery C (1924) Hymenoptera, Fam. Formicidae, subfam. Myrmicinae. In: Wytsman P. Genera Insectorum. Fasc. 174C (1922), Bruxelles, 207–397.

Forel A (1917) Cadre synoptique actuel de la faune universelle des fourmis. Bulletin de la Société Vaudoise des Sciences Naturelles 51: 229–253.

Handlirsch A (1907) Die Fossilen Insekten und die Phylogenie der Rezenten Formen. Ein Handbuch für Paläontologen und Zoologen. 6 Lieferung, Leipzig: 801–960. https://doi.org/10.5962/bhl.title.34145

Keilbach R (1982) Bibliographie und Liste der Arten tierischer Einschlüsse in fossilen Harzen sowie ihrer Aufbewahrungsorte. Deutsche Entomologische Zeitschrift (N.F.) 29: 129–286. https://antwiki.org/wiki/images/f/f5/Keilbach_1982.pdf

Mayr G (1868) Die Ameisen des baltischen Bernsteins. Beiträge zur Naturkunde Preussens Königlichen Physikalisch-Ökonomischen Gesellschaft zu Königsberg 1: 1–102.

Perkovsky EE (2016) Tropical and Holarctic ants in Late Eocene ambers. Vestnik zoologii 50: 111–122. https://doi.org/10.1515/vzoo-2016-0014

Radchenko A (2023) *Myrmica* ants (Hymenoptera, Formicidae) in late Eocene European ambers. Annales Zoologici 73: 629–648. https://doi.org/10.3161/00034541ANZ2023.73.4.006

Radchenko A (2024) *Eotemnothorax* gen. nov. (Hymenoptera, Formicidae) – a new ant genus from late Eocene European ambers. Annales Zoologici 74: 717–752. https://doi.org/10.3161/00034541ANZ2024.74.4.015

Radchenko A, Dlussky GM (2012) *Boltonidris* gen. nov., the first extinct Stenammini ant genus (Hymenoptera, Formicidae) from the late Eocene Rovno Amber. Annales Zoologici 62(4): 627–631. https://doi.org/10.3161/000345412X659687

Radchenko A, Dlussky GM (2015) First record of fossil species of the genus *Tetramorium* Mayr (Hymenoptera, Formicidae). Vestnik zoologii 49(4): 311–316. https://doi.org/10.1515/vzoo-2015-0033

Radchenko A, Dlussky GM (2017a) Further records of the extinct ant genus *Enneamerus* Mayr (Hymenoptera, Formicidae) from the Late Eocene European ambers. Asian Myrmecology 9: 1–11. https://doi.org/10.20362/am.009012

Radchenko A, Dlussky GM (2017b) New species of the extinct ant genus *Stigmomyrmex* Mayr and designation of the neotype of *Stiphromyrmex robustus* (Mayr) (Hymenoptera, Formicidae, Myrmicinae). Annales Zoologici 67: 773–780. https://doi.org/10.3161/00034541ANZ2017.67.4.012

Radchenko A, Dlussky GM (2018) Two new fossil species of the ant genus *Pristomyrmex* Mayr (Hymenoptera, Formicidae) from the Rovno and Bitterfeld ambers. Annales Zoologici 6: 251–258. https://doi.org/10.3161/00034541ANZ2018.68.2.004

Radchenko A, Dlussky G, Elmes GW (2007) The ants of the genus *Myrmica* (Hymenoptera, Formicidae) from Baltic and Saxonian amber (late Eocene). Journal of Paleontology 81(6): 1494–1501. https://doi.org/10.1666/05-066.1

Radchenko AG, Gröhn C, Ribbecke H-W (2024) Two new *Aphaenogaster* species (Hymenoptera, Formicidae) from Baltic Amber. Zoodiversity 58: 195–202. https://doi.org/10.15407/zoo2024.03.195

Radchenko A, Khomych M (2025) The oldest know *Cardiocondyla* ant (Hymenoptera, Formicidae) from the late Eocene Rovno amber (Ukraine). Palaeoentomology 8(3): 307–315. https://doi.org/10.11646/palaeoentomology.8.3.7

Radchenko AG, Khomych MR, Kalmer MM (2025) First record of *Bradoponera wunderlichi* (Hymenoptera, Formicidae) from Rovno amber, with description of the worker caste. Zoodiversity 59: 113–120. https://doi.org/10.15407/zoo2025.02.113

Scudder SH (1891) Index to the known fossil insects of the world, including myriapods and arachnids. Bulletin of the United States Geological Survey 71: 1–744. https://doi.org/10.5962/bhl.title.34455

Ward PS, Brady SG, Fisher BL, Schultz TR (2015) The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade. Systematic Entomology 40: 61–81. https://doi.org/10.1111/syen.12090

Wheeler WM (1915) The ants of the Baltic Amber. Schriften der Physikalisch-Ökonomischen Gesellschaft zu Königsberg in Preußen 55: 1–142. https://www.antwiki.org/w/images/e/ec/Wheeler_1915i.pdf